SIX NEW SPECIES OF *NIRRIDESSUS* WATTS AND HUMPHREYS AND *TJIRTUDESSUS* WATTS AND HUMPHREYS (COLEOPTERA: DYTISCIDAE) FROM UNDERGROUND WATERS IN AUSTRALIA

C. H. S. WATTS AND W. F. HUMPHREYS

WATTS, C. H. S. and HUMPHREYS, W. F. 2000. Six new species of *Nirridessus* Watts and Humphreys and *Tjirtudessus* Watts and Humphreys (Coleoptera: Dytiscidae) from underground waters in Australia. *Records of the South Australian Museum* 33(2): 127–144.

Six new species (*Nirridessus bigbellensis, N. cueensis, N. hinkleri, N. morgani, Tjirtudessus hahni* and *T. magnificus*) of stygobiontic beetles of the family Dytiscidae, subfamily Hydroporinae, tribe Bidessini, from relatively shallow, calcrete aquifers in Western Australia, are described and figured. The species are members of a diverse, recently discovered, relictual stygofauna, predominantly of Crustacea and Oligochaeta, inhabiting calcretes lying along palaeodrainage channels. The two genera occur in palaeochannel deposits on either side of the divide between the inland and Indian Ocean drainages. Each calcrete area contains a distinct assemblage of beetles and the fauna occurs in both fresh and saline groundwater. The physico-chemical properties of the groundwater, and the palaeogeography and hydrology of the region are discussed in some detail.

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Stygobiotic water beetles have been reported from a number of widely scattered localities around the world (Spangler 1986) but it was not until 1999 that they were first reported from Australia (Watts and Humphreys 1999). These belonged to the Dytiscidae and were discovered living in relatively shallow calcrete aquifers in the Lake Way/Lake Carey palaeodrainage system of Western Australia. Five species in three genera in the tribe Bidessini were involved.

These groundwater calcretes are restricted to the arid parts of Australia (Fig. 40) where the potential evaporation exceeds rainfall by more than an order of magnitude (detailed in Humphreys 1999; Watts and Humphreys 1999).

In May 1999 one of us (W.F.H.) spent some time investigating other areas of inland palaeodrainage in Western Australia with groundwater calcretes and discovered additional stygofaunas which included dytiscids.

In this paper we describe the six species of Dytiscidae collected and record the existence of a further two, all belonging to two of the original genera: *Tjirtudessus* and *Nirridessus.* We also give details of the physico-chemical properties of the water in the aquifers and the palaeogeography and hydrology of the region.

METHODS

About 120 sites were sampled, comprising pastoral wells and boreholes constructed for water abstraction, groundwater investigation and mineral exploration in a number of fractured rock, alluvial and groundwater calcrete aquifers from the central Yilgarn Craton of Western Australia (Fig. 38). The beetles and associated fauna were taken by plankton nets hauled through the water column of the bores and wells, or sometimes from baited traps.

Physico-chemical parameters in the water were determined either *in situ*, or in a sample taken near the surface using a bailer, using electronic instruments—pH using a WTW pH 320 meter with a SenTix 97T pH combined electrode with integrated temperature sensor and redox probe, and dissolved oxygen using a WTW Oxi 320 meter and a CellOx 325 oxygen sensor (Wissenschaftlich-Technisch Werkstatten GmbH, Weilheim, Germany). Conductivity was measured with a TPS Model LC 84 conductivity meter (TPI Electronics, Springwood, Queensland, Australia). All were calibrated as specified using the recommended standards. In some samples the salinity was determined using a hand refractometer (Atago S-10e).

Abbreviations used

BES Prefix for field numbers, WAM Biospeleology.

OB Observation bore.

PAT Prefix, observation bore number, Austin Downs Borefield, Big Bell Mine.

SB Prefix, piezometer number in Hinkler Well calcrete to the west of Lake Way.

TPB Prefix, piezometer number in Hinkler Well calcrete to the west of Lake Way.

SAMA South Australian Museum, Adelaide.

WAM Western Australian Museum, Perth.

Systematics

Key To Australian Species Of Stygobionic Bidessini

1. — Body length <1.2 mm, dorsal surface strongly reticulate, legs stout, without swimming-hairs on fore and midlegs .... *Kintingka kurutjutu* Watts & Humphreys

— Body length >1.2 mm, dorsal surface with weak to moderate reticulation, legs normal, all legs with swimming hairs 2

2. — Pronotum usually wider than elytra (Fig. 1); third and fourth (apical) segments of labial palpi subequal in length (Figs 23–25); setae on hind edge of mesofemur not greatly different in robustness from those on mesotrochanter (Figs 10, 19, 20). Length > 3.0 mm .... (*Tjirtudessus*) 9

— Pronotum same width or narrower than elytra (Figs 3–6); third segments of labial palpi half to two thirds length of apical (Figs 26–32); setae on hind edge of mesofemur near base much more robust than those on mesotrochanter or elsewhere on femur (Figs 7–9). Length 1.0–3.2 mm .... (*Nirridessus*) 3

3. — Pronotal plicae well marked 4

— Pronotal plicae difficult to trace 5

4. — Length of metatarsal segments 1 & 2 > segments 3 & 4; eye remnant present; parameres with long apical lobe .... *N. pulpa* Watts & Humphreys

— Length of metatarsal segments 1 & 2 = < segments 3 & 4; without eye remnant; parameres with small apical lobe (Fig. 33) .... *N. morgani* sp. nov.

5. — Length => 3.0 mm; eye remnant present (Fig. 5); group of six spines close to base of mesofemur on hind edge (Fig. 11) .... *N. bigbellensis* sp.nov.

— Length =< 2.5 mm; with or without eye remnant; spines on mesofemur spread out along hind edge or, if restricted to base, four or fewer (Figs 8, 9, 13, 15) 6

6. — Pro- and mesotarsi broad (Fig. 4); segments two and three of antennae similar in shape; apical lobe of paramere overlies part of rest of paramere (Fig. 34) .... *N. cueensis* sp.nov.

— Pro- and mesotarsi only weakly expanded (Fig. 3); segments two and three of antennae different in shape, second broad and rounded, third narrow and triangular; apical lobe of paramere well separated from rest of paramere (Fig. 35) 7

7. — Elytron without subsutural row of punctures; metatrochanters bluntly pointed (Fig. 14); length approximately 1.5 mm; median lobe of aedeagus truncated (Fig. 35) .... *N. hinkleri* sp.nov.

— Elytron with row of large subsutural punctures; metatrochanters rounded; length up to 2.5mm; median lobe of aedeagus pointed 8

8. — Length 2.2–2.3 mm; with eye remnant...... .. *N. windarraensis* Watts & Humphreys

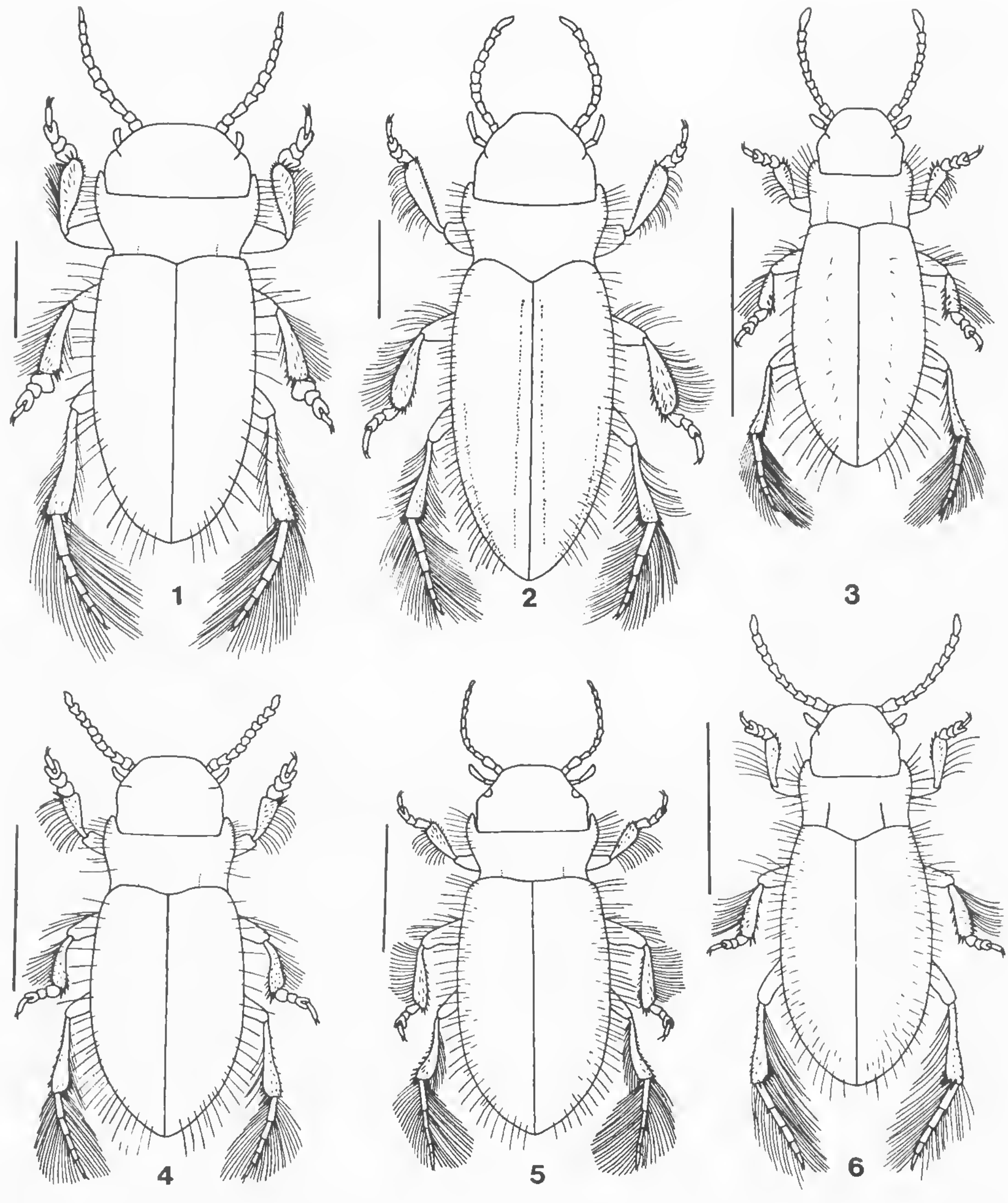
— Length 1.3–1.5 mm; without eye remnant .... *N. lapostaae* Watts & Humphreys

9. — Pro- and mesotarsi strongly expanded (Fig. 1); apical five segments of antennae noticeably thinner than others (Fig. 1) ... . *T. magnificus* sp. nov.

— Pro- and mesotarsi only moderately expanded (Fig. 2); apical five segments of antennae not narrower than others (Fig. 2) 10

10. — Length > 4.0mm; median lobe of aedeagus twisted, tip knobbed (Fig. 37); without eye remnant; pronotum at its base a little narrower than elytra (Fig. 2) .... *T. hahni* sp. nov.

— Length < 4.0mm; median lobe of aedeagus not twisted, tip pointed; with small eye remnant; pronotum at its base wider than elytra .... *T. eberhardi* Watts & Humphreys



FIGURES 1–6. **1**, Dorsal view of *Tjirtudessus magnificus*; **2**, ditto *T. hahni*; **3**, ditto *Nirridessus hinkleri*; **4**, ditto *N. cueensis*; **5**, ditto *N. bigbellensis*; **6**, ditto *N. morgani*. Scale bar = 1mm.

Tjirtudessus Watts & Humphreys, 1999

Tjirtudessus magnificus sp. nov.

Types

Holotype: m. 'BES 7040, Old Cue water supply bore, 27°16'10"S, 117°59'23" E, 12/5/99, coll W. F. Humphreys & H. J. Hahn', in spirit, WAM, registration number 26840.

Paratype: f. BES 7066, same data as for holotype except 13/5/99, SAMA.

Description (number examined, 2) Figs 1, 19, 20, 25, 36.

Habitus: Length 4.7–4.8 mm.; relatively flat, strongly constricted at junction of pronotum/elytra; uniformly light testaceous; hindwing vestigial, about half length of elytron (Fig 1).

Head: Large, nearly as wide as elytra; smooth, reticulation very fine, punctures sparse, weak; subparallel in posterior half; sides with dark suture in middle near anterior edge. Antenna relatively stout, basal two segments cylindrical, third segment longer and narrower at base, next three subequal, next four progressively thinner, apical segment a bit longer and much narrower than penultimate, each segment with some very small setae on inside apically (Fig. 1). Maxillary palpus thin, elongate, apical segment large, a little shorter than segments one to three combined, three long setae on outer side and some sensillae towards tip, tip truncated. Labial palpus moderate, apical two segments subequal, tip weakly bifid, penultimate segment with small papilla near tip bearing two setae (Fig. 25).

Pronotum: Very broad, wider than elytra (Fig. 1); anterolateral angles projecting strongly forward; base quite strongly narrowed, posterolateral angles acute; smooth, with sparse, very weak punctures and a row of stronger punctures along front margin; basal plicae weak, reaching to about half way along pronotum, slightly excavated inwards; with row of long setae laterally, denser towards front.

Elytra: Not fused, lacking inner ridges; elongate, widest behind middle, smooth, quite densely and evenly covered with very small punctures, row of widely spaced larger punctures close to inner edge; lacking setiferous micropunctures; row of long setae near lateral edge, a few additional larger punctures with long setae, more frequent towards sides. Epipleuron broad in anterior fifth, then rapidly narrowing to be virtually absent over rest of elytron.

Ventral surface: Prothoracic process relatively broad, strongly narrowed between coxae, not reaching mesothorax, apical half spatulate, strongly arched in lateral view with highest point (viewed ventrally) between coxae. Mesocoxae in contact at midline. Metathorax sharply triangular in front in midline, wings very narrow, broadly rounded in midline behind. Metacoxal plates large, metacoxal lines short, weak, widely spaced, reaching to about halfway to metasternum, diverging in anterior two-thirds; moderately covered with small setae-bearing punctures; closely adpressed to first abdominal ventrite. First and second ventrites fused, sutural lines distinct, ventrites three to five mobile, moderately covered with small seta-bearing punctures, ventrites three and four with a long central seta or bunch of long setae.

Legs: Protibia relatively narrow, inner edge straight, outer edge bowed, widest past middle where it is about three times its basal width; protarsi greatly expanded, first segment very broadly oval, second segment broad about one third length of first, third segment as long as first but much narrower and very deeply bifid, fourth segment very small and hidden within lobes of third segment, apical segment narrow, cylindrical, about length of third, segments one to three with very dense covering of adhesive setae; claws short and simple. Mesotrochanter rounded with row of setae on inner edge; mesofemur with row of 10–12 relatively weak setae along hind edge in basal half (Fig.19); mesotarsi similar to protarsi. Metatrochanter weakly pointed (Fig. 20); metafemur elongate, lacking spines; metatibia strongly curved, widening towards apex; metatarsi elongate, basal segment longest, apical segment a little longer than fourth, segments one and two in combination about as long as others; claws weak.

Male: Antennae a little stouter; pro- and mesotarsi a little stouter. Median lobe of aedeagus narrow, narrowing rapidly in apical quarter; paramere broad, apical segment with pronounced, narrow, apical lobe (Fig. 36).

Etymology

The species is named in reference to its appearance.

Remarks

A very large broad flat *Tjirtudessus* readily recognised by the large round first segment of the pro- and mesotarsi of both sexes, and the distinctive antennae with the apical segments noticeably narrower than the middle segments.

Tjirtudessus hahni sp. nov.

Types

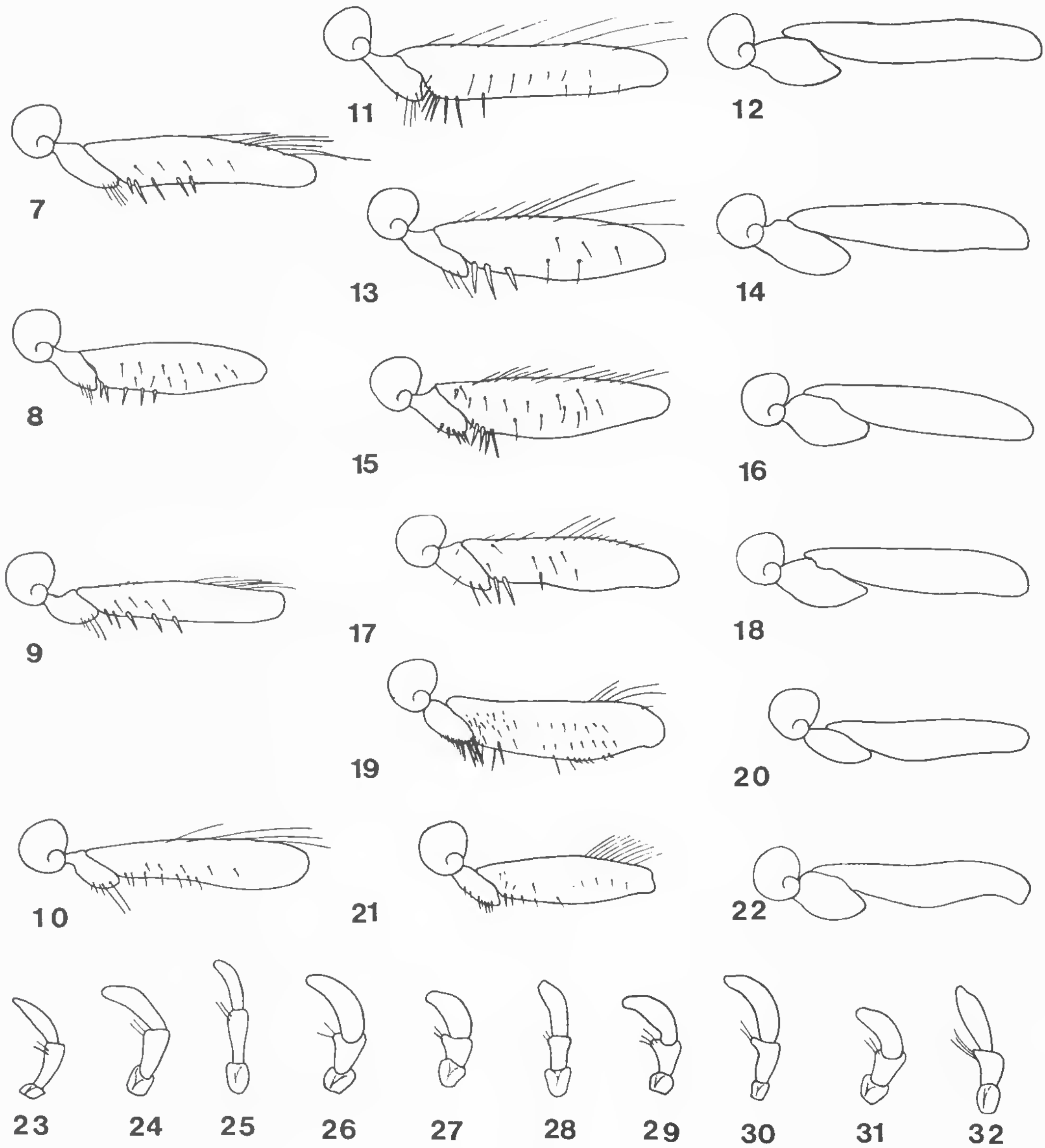
Holotype: m. 'BES 7197, mineral exploration bore, 26°41'16"S, 120°17'52"E, 21/5/99, coll. W. F. Humphreys & H. J. Hahn', slide mounted, WAM, registration number 26887.

Paratypes: 4; same data as holotype, most incomplete, 2 slide mounted, SAMA, 2 in spirit, WAM, registration numbers 26841, 26842.

Description (number examined, 5) Figs 2, 21, 22, 24, 37.

Habitus: Length 4.8 mm.; relatively flat, strongly constricted at junction of pronotum/elytra; uniformly light testaceous; hindwing vestigial, about one-third length of elytron (Fig. 2).

Head: Large, smooth, reticulation very fine, punctures sparse, weak; subparallel in posterior



FIGURES 7–32. **7**, Ventral view of mesotrochanter and mesofemur of *Nirridessus pulpa*; **8**, ditto *N. windarraensis*; **9**, ditto *N. lapostaae*; **10**, ditto *Tjirtudessus eberhardi*; **11–12**, ventral views of mesotrochanter and mesofemur and metatrochanter and metafemur of *N. bigbellensis*; **13–14,** ditto *N. hinkleri*; **15–16**, ditto *N. cueensis*; **17–18**, ditto *N. morgani*; **19–20** ditto *T. magnificus*; **21–22**, ditto *T. hahni*; **23,** labial palpus of *T. eberhardi*; **24**, ditto *T. hahni*; **25**, ditto *T. magnificus*; **26**, ditto *N. bigbellensis*; **27**, ditto *N. hinkleri*; **28**, ditto *N. morgani*; **29**, ditto *N. cueensis*; **30**, ditto *N. windarraensis*; **31**, ditto *N. lapostaae*; **32,** ditto *N. pulpa*.

half; sides with dark suture in middle near anterior edge. Antenna stout, basal two segments largest, next six segments narrower at base, subequal, segment six the widest, apical segment twice as long as penultimate (Fig. 2); each segment with some very small setae on inside apically. Maxillary palpus relatively thin, elongate; apical segment largest, some sensillae towards tip, tip weakly bifid. Labial palpus not particularly thin; apical two segments subequal; tip weakly bifid; penultimate segment with two setae near apex arising from slight bulge (Fig. 24).

Pronotum: Broad, a little narrower than elytra (Fig. 2); anterolateral angles projecting strongly forward; base quite strongly narrowed; posterolateral angles acute; smooth, punctures sparse, very small, a row of stronger punctures along front margin; basal plicae short, very weak, only visible in some lights; row of long setae laterally, denser towards front.

Elytra: Not fused; lacking inner ridges; elongate, widest behind middle. Elytron smooth, quite densely and evenly covered with small punctures each with a small seta, row of widely spaced larger punctures close to inner edge; some setiferous micropunctures at base, near suture and near apex; row of long setae near lateral edge, a few additional long setae, more frequent towards sides. Epipleuron broad in anterior fifth, then rapidly narrowing to be virtually absent over rest of elytron.

Ventral surface: Prothoracic process relatively broad, strongly narrowed between coxae, not reaching mesothorax, apical half spatulate, tip rounded, strongly arched in lateral view with highest point (viewed ventrally) between coxae. Mesocoxae meet. Metathorax sharply triangular in front in midline, wings very narrow, broadly rounded in midline behind. Metacoxal plates large; metacoxal lines short, weak, widely spaced, almost obsolete; punctures very sparse, very weak; closely adpressed to first abdominal ventrite. First and second ventrites fused, sutural line virtually obliterated, ventrites three to five mobile, moderately covered with small seta-bearing punctures, ventrites three and four with a long central seta or bunch of long setae.

Legs: Protibia moderately broad, inner edge straight, outer edge bowed, widest past middle where it is about three times its basal width; protarsi weakly expanded, second segment about half length of first, third segment equal in length to first, fourth segment very small and hidden within deeply lobed third segment, apical segment long, thin, segments one to three with dense covering of adhesive setae, claws relatively strong, simple. Mesotrochanter parallel-sided broadly triangular at apex with a few setae on inner edge, mesofemur with a row of five to six relatively weak setae along hind edge in basal half (Fig. 21); mesotarsi more elongate than protarsi. Metatrochanter curved on outer edge straight on inner edge (Fig. 22), metafemur elongate, sinuate (Fig. 22), metatibia weakly curved, widening towards apex; metatarsi elongate, basal segment longest, apical segment a little longer than fourth, segments one and two in combination about as long as others; claws weak.

Male: Antennae and tarsi as in female. Median lobe of aedeagus narrow, twisted slightly, knobbed at apex; paramere broad, two-segmented, apical segment with pronounced, narrow, apical lobe (Fig. 37).

Etymology

This species is named after Hans Jurgen Hahn who assisted with describing the physicochemical environment occupied by the stygofauna. The type locality is an excellent example of this kind of habitat.

Remarks

T. hahni resembles *T. magnificus* in its large size and broad body but differs in its much less expanded pro- and mesotarsi and in its more normal antennae which have segments 5–10 subequal in size. It can be separated from both *T. magnificus* and *T. eberhardi* by the median lobe of the aedeagus which is noticeably twisted and has a rounded knob at the tip and by its pronotum which, unlike in those species, is a little narrower than the elytra.

Nirridessus Watts & Humphreys, 1999.

Nirridessus hinkleri sp. nov.

Types

Holotype: m. 'BES 7134, SB 32/1, 26°52'31"S, 120°12'05"E, 17/5/99, coll. W. F. Humphreys & H. J. Hahn', slide mounted, WAM, registration number 26843.

Paratypes: 58, same data as holotype, 29 WAM, registration number 26844, 28 SAMA; 3, 'BES 7130, TPB25/4, 26°52'50"S, 120°09'44"E, 17/5/99', 1 WAM, registration number 26845, 2 SAMA; 3, 'BES 7218, 26°51'37"S, 120°18'05"E, 22/5/99', 2 WAM, registration numbers 26846, 26847, 1 SAMA; 34, 'BES 7137, SB32/1, 26°52'31"S 120°18'05"E', 12 WAM, registration number 26848, 15 SAMA; 3, 'BES 7136, 26°52'31"S 120°12'05"E', WAM, registration numbers 26849, 26850, 26851; 1, 'BES 7166, 26°41'14"S 120°18'09"E', WAM, registration number 26852; 2, BES 7228, 1 WAM, registration number 26853, 1 SAMA. All collected by W. F. Humphreys & H. J. Hahn.

Additional specimen

The following partial specimen probably belongs to this species. BES 7222 Hinkler calcrete east, 26°51'36"S, 120°18'05"E, 22/5/99, coll. W. F. Humphreys & H. J. Hahn. WAM registration number 26854.

Description (number examined, 106) Figs 3, 13, 14, 27, 35.

Habitus: Length 1.4–1.8 mm.; relatively flat, elongate, pronotum narrowing at base; uniformly very light testaceous; hindwing vestigial, reduced to about one half length of elytron.

Head: Broad, parallel sided in basal half, rapidly narrowing forward of area where eye would be; a short dark suture at each side in middle at edge; reticulation moderate; punctures sparse, weak, row of setiferous punctures running backwards from above antennal base. Antenna moderately stout (Fig. 3), basal segment parallel sided, second segment rounded, third much narrower than second, fourth much shorter, then approximately the same size until penultimate, apical segment thinner and about twice as long as penultimate, a few small setae near apex of each segment. Tip of last segment of maxillary palpus very weakly bifid, a few small setae towards tip, penultimate segment much shorter than apical, with small papilla bearing two setae near apex (Fig. 27).

Pronotum: A little narrower than elytra (Fig. 3), broad in front, narrowing behind, strongly extended forward at anterolateral angles, posterolateral angles acute; punctures very sparse, weak, a few larger punctures towards front edge; moderately reticulate; basal plicae weak, straight, reaching about half way along pronotum; row of long, thin setae in front half at edges and on forward extensions.

Elytra: Not fused but tightly locked; lacking inner ridges; widest in middle; punctures very fine, very sparse, each with a small seta, a few punctures with longer setae; moderately reticulate; moderately covered with micropunctures at base, near suture and apex; sides of elytra quite strongly vertical, with row of long thin setae at edge, denser towards front. Epipleuron present in anterior quarter, absent in apical half.

Ventral surface: Pronotal process arched in lateral view, highest point (viewed ventrally) between coxae, apical half roughly parallel-sided, bluntly pointed, narrowing between coxae, not reaching metathorax. Mesocoxae in contact in midline. Metathorax with a few very small punctures; quite sharply triangular in midline in front; wings very narrow, subobsolete; narrowing to a broad point behind in midline. Metacoxal lines, well separated, weakly diverging, reaching to about halfway to mesosternum; sparsely punctate; adpressed to first abdominal ventrite. Metacoxal plates and first and second ventrites fused but sutures evident, other ventrites free, sternites three and four with central group of setae, otherwise virtually without setae; virtually impunctate.

Legs: Protibia relatively thin, about four times as broad at apex than at base; protarsi weakly expanded, second segment about a quarter the length of first, fourth segment very small, hidden within deeply bilobed third segment, adhesive setae sparse, weak; claws weak. Mesotrochanter relatively large, rounded with a few setae on inner edge; mesofemur with three to four strong spines on hind edge restricted to basal half but not all grouped near base (Fig. 13); mesotarsi less strongly expanded than protarsi. Metatrochanter large, outer edge curved, inner edge straight, weakly pointed, well separated from femur at apex (Fig. 14); metafemur relatively narrow, anterior edge weakly sinuate, impunctate, without spines; metatibia strongly curved, thickening apically; metatarsal segments elongate, progressively smaller towards apical segment which is a little longer than penultimate, combined length of basal two segments approximately equal to other three; claws weak, outer one slightly smaller than inner.

Male: Appendages and legs as for female. Median lobe of aedeagus moderately broad, concave above, tip broadly rounded with small central point; parameres moderately broad, two segmented, apical segment with pronounced narrow apical portion (Fig. 35).

Etymology

The name pertains to the Hinkler Well Catchment in which the classic study of the hydrogeochemistry of ground water calcretes was undertaken (Mann and Deutscher 1978).

Remarks

This is a small species with a distinctive aedeagus. The pointed rather than rounded metatrochanters and acute rather than rectangular posterolateral angles to the pronotum, will separate it from the similar sized *N. lapostaae*.

Nirridessus cueensis sp. nov.

Types

Holotype: m. 'BES 7040, Old Cue water supply bores, 27°16'11"S, 117°59'23"E, 12/5/99, coll W. F. Humphreys & H. J. Hahn', slide mounted, WAM, registration number 26856.

Paratypes: 6, same data as holotype, 2 SAMA, 4 WAM, registration numbers 26857, 26858, 26859, 26860; 8, same data as holotype except for, 'BES 7067, 13/5/99', 4, SAMA 4, WAM, registration numbers 26861, 26862, 26863, 26864; 2, same data as holotype except for 'BES 7038', WAM, registration numbers 26865, 26866.

Description (number examined, 18) Figs 4, 15, 16, 29, 34.

Habitus: Length 2.1–2.4 mm.; relatively flat, elongate, pronotum a little narrower than elytra, constricted at base; uniformly very light testaceous; hindwing vestigial, reduced to about one half length of elytron.

Head: Broad, parallel sided in basal half, rapidly narrowing forward of area where eye would be; a short dark suture at each side in middle at edge; reticulation very weak; punctures sparse, weak, row of setiferous punctures running backwards from above antenna base. Antenna stout, robust, basal segment cylindrical, second more elongate, third smaller narrowing to base, then progressively widening until penultimate, apical segment thinner and slightly longer, a few small setae near apex of each segment. Last segment of maxillary palpus relatively broad, tip weakly bifid, a few small setae towards tip. Penultimate segment of labial palpus with strong cone-like projection near apex bearing two setae, approximately two thirds length of apical (Fig. 29).

Pronotum: Same width or a bit narrower than elytra, broad in front, narrowing quite markedly behind, strongly extended forward at anterolateral angles, posterolateral angles rectangular; punctures sparse, weak; weakly reticulate; two fine, basal plicae weakly impressed, straight, reaching about a half way along pronotum; row of long, thin setae in front half at edges and on forward extensions.

Elytra: Not fused but tightly locked, lacking inner ridges; widest in middle; punctures very fine, sparse, each with a small seta, a few punctures with longer setae; a few micropunctures near apex; sides of elytra quite strongly vertical; with row of long thin setae at edge, denser towards front. Epipleuron broad in front, narrowing quite rapidly to level of first sternite, then thin to apex, difficult to differentiate from disc.

Ventral surface: Pronotal process arched in lateral view, highest point (viewed ventrally) between coxae, apical half broadly spatulate, narrowing between coxae, not reaching metathorax. Mesocoxae in contact in midline. Metathorax with a few very small punctures; quite sharply triangular in midline in front; wings very narrow, subobsolete; rounded behind. Metacoxal plates with weakly raised central portion; metacoxal lines weak, well separated, diverging in anterior third, reaching to about halfway to mesosternum; sparsely punctate; adpressed to first abdominal ventrite. Metacoxal plates and first and second ventrites fused but sutures evident, other ventrites free, ventrites three and four with central group of setae, otherwise virtually without setae; virtually impunctate.

Legs: Protibia about three times as broad at apex than at base; protarsi moderately expanded, second segment half length of first, third segment deeply bilobed, a little longer than first, fourth segment very small and hidden within bilobed third segment, adhesive setae moderately dense; claws moderate. Mesotrochanter rounded at tip with some setae on inner edge (Fig. 15); mesofemur with three to five strong spines on hind edge grouped together near base (Fig.15); mesotarsi similar to protarsi. Metatrochanter large, outer edge rounded, inner edge straight, weakly separated from femur at apex (Fig.16); metafemur relatively narrow, anterior edge weakly sinuate, impunctate, without spines; metatibia strongly curved, thickening apically; metatarsal segments elongate, progressively smaller towards apical segment which is a little longer than penultimate, combined length of basal two segments approximately equal to other three; claws weak, outer one slightly smaller than other.

Male: Appendages and legs as above. Median lobe of aedeagus moderately broad, concave above, narrowing rapidly close to tip, small brush of setae dorsally near tip; parameres moderately broad, apical segment with pronounced narrow apical portion which partly overlaps basal portion (Fig. 34).

Etymology

This species is named after the type locality.

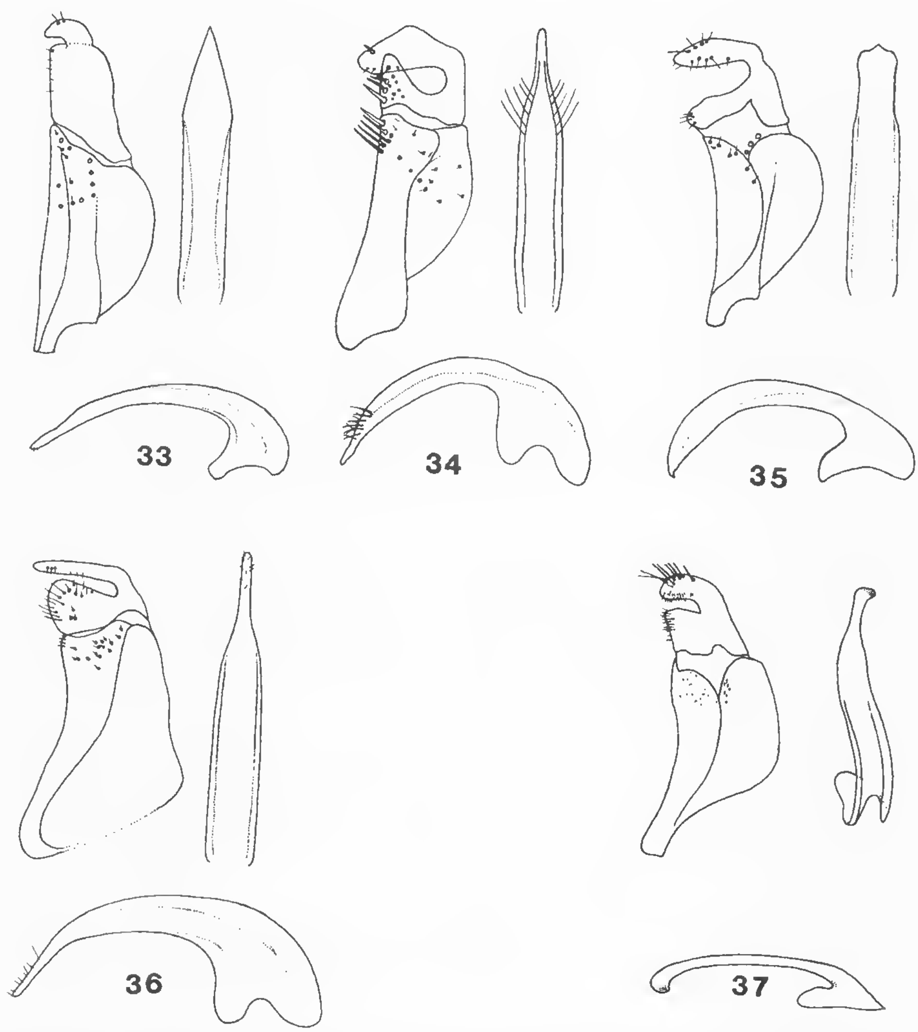
Remarks

Nirridessus cueensis seems close to *N. lapostaae* but is larger, its pro- and mesotarsi are much broader and its metatrochanters are not as rounded. The spines/strong setae on the hind edge of the mesofemur are grouped together near the base whereas in *N. lapostaae* they are more spread out along the basal half of the femur. The aedeagus differs from most *Nirridessus* by having a group of setae near the apex. The parameres are unique in *Nirridessus* in having the apical lobe overlapping part of the rest of the paramere and with strong spines on the inner edge (Fig. 34).

Nirridessus morgani sp. nov.

Types

Holotype: m. 'BES 7192, Sample 2 Site 284,



FIGURES 33–37. **33**, Paramere, dorsal view of central lobe and lateral view of central lobe of aedeagus of *Nirridessus morgani*; **34**, ditto *N. cueensis*; **35**, ditto *N. hinkleri*; **36**, ditto, *Tjirtudessus magnificus*; **37**, ditto *T. hahni*.

mineral exploration bore, 26°41'15"S, 120°21'10"E; 21/5/99, coll W. F. Humphreys & H. J. Hahn', in spirit, WAM, registration number 26867.

Paratypes: 6, as for holotype, 4 SAMA, 2 WAM, registration numbers 26868, 26869; 5, 'BES 7171, Site 262, mineral exploration bore, Lake Way, 26°68'74"S 120°35'31"E, 19/5/99', 1 SAMA, 4 WAM, registration numbers 26870, 26871, 26872, 26873.

Description (number examined, 10) Figs 6, 17, 18, 28, 33.

Habitus: Length 2.1–2.2 mm; relatively flat but deep bodied, elongate, pronotum weakly narrowing at base; uniformly very light testaceous; hindwing vestigial, reduced to about one half length of elytron.

Head: Relatively narrow, parallel sided in basal half, rapidly narrowing forward of area where eye would be; a short dark suture at each side in middle at edge; very weak reticulation; punctures sparse, weak, row of setiferous punctures running backwards from above antenna base; weakly reticulate. Antenna relatively stout, basal two segments broad, third narrower, fourth similar to third, then approximately equal in size until penultimate, apical segment a bit longer but same width, a few small setae near apex of each segment. Tip of last segment of maxillary palpus weakly bifid, a few small setae towards tip. Penultimate segment of labial palpus shorter than apical, with two setae on slight bulge near apex (Fig. 28).

Pronotum: Much narrower than elytra, narrower behind, strongly extended forward at anterolateral angles, posterolateral angles square; punctures very sparse weak, a few larger punctures towards front edge; two strongly raised basal plicae, straight, reaching about half way along pronotum; row of long, thin setae in front half at edges and on forward extensions.

Elytra: Fused but may open slightly in preparations, lacking inner ridges; sides subparallel in middle; punctures very fine, sparse, each with a small seta, a few punctures with longer setae; moderately covered with micropunctures particularly at base, near suture and apex; sides of elytra quite strongly vertical; with row of long thin setae at edge, denser towards front. Epipleuron broad in front quarter, narrowing quite rapidly to middle, absent in apical half.

Ventral surface: Pronotal process arched in lateral view, highest point (viewed ventrally) between coxae, apical half parallel sided, tip weakly and bluntly pointed, narrowing between coxae, not reaching metathorax. Mesocoxae in contact in midline. Metathorax with a few small punctures; broadly triangular in midline in front; wings very narrow; narrowing to blunt point behind. Metacoxal plate with weakly raised central portion; metacoxal lines well separated, progressively diverging, reaching to about halfway to mesosternum; sparsely punctate; adpressed to first abdominal ventrite. Metacoxal plates and first and second ventrites fused but sutures evident, other ventrites free, ventrites three and four with central group of setae, otherwise virtually without setae; virtually impunctate.

Legs: Protibia about three times as broad at apex than at base; protarsi weakly expanded, second segment not much shorter than first, the fourth segment very small and hidden within deeply bilobed third segment, adhesive setae sparse; claws weak. Mesotrochanter sharply pointed, without setae on inner edge; mesofemur with two strong setae on hind margin at base (Fig. 17); mesotarsi slightly less strongly expanded than protarsi. Metatrochanter large, completely exposed, pointed, close to metafemur at apex (Fig. 18); metafemur relatively narrow, anterior edge weakly sinuate, impunctate, without spines; metatibia curved, thickening apically; metatarsal segments elongate, progressively smaller towards apical segment which is a little longer than penultimate, combined length of basal two segments approximately equal to other three; claws weak, outer one slightly smaller than other.

Male: Appendages and legs as for female. Median lobe of aedeagus moderately broad, concave above, narrowing to tip, without setae; parameres moderately broad, apical segment relatively long with small apical lobe (Fig. 33).

Etymology

This species is named after Kevin Morgan for his understanding of the hydrology and geochemistry of the palaeodrainage channels in Western Australia (Morgan 1993).

Remarks

The well marked pronotal plicae and pointed metatrochanters suggest a relationship with *N. pulpa*. The lack of an eye remnant and thinner antennae will separate it from this species. The distinctive, small, apical lobe on the paramere and the group of strong spines on the hind edge of the mesofemur reduced to two will separate it from all other *Nirridessus*.

Nirridessus bigbellensis sp. nov.

Types

Holotype: f. 'BES 7050, borefield monitoring bore PAT 7, Austin Downs Pastoral Station, 27°24'48"S 117°42'40"E, 12/5/99', coll. W. H. Humphreys & H. J. Hahn', slide mounted, WAM, registration number 26874.

Paratype: f. (partial specimen) as for holotype, slide mounted, SAMA.

Description (number examined, 2) Figs 5, 11, 12, 26.

Habitus: Length 3.0–3.2 mm.; relatively flat and broad, pronotum weakly narrowing at base; uniformly very light testaceous; hindwing vestigial, reduced to about two-thirds length of elytron.

Head: Broad, parallel sided in basal half, rapidly narrowing forward of area where eye would be; a small oval area delineated by dark sutures at each side in middle at edge; very weak reticulation; punctures sparse, weak, row of setiferous punctures running backwards from above antennal base. Antenna relatively thin, basal two segments broadest, third as long as second but narrower, fourth shorter, then approximately equal in size until apical segment which is longer and thinner than penultimate, a few small setae near apex of each segment. Maxillary palpus relatively thin, apical segment as long as other three combined, tip of last segment truncated, a few small setae towards tip. Apical segment of labial palpus twice length of penultimate which has two setae on slight bulge near apex (Fig. 26).

Pronotum: Broad, narrower than elytra, strongly constricted near base, strongly extended forward at anterolateral angles, posterolateral angles acute; punctures very sparse, weak, a few larger punctures towards front edge; basal plicae subobsolete; row of long, thin setae in front half at edges and on forward extensions.

Elytra. Not fused, lacking inner ridges; sides rounded; punctures small, very sparse, setiferous, a few punctures with longer setae; some micropunctures near apex; row of long thin setae laterally, denser towards front. Epipleuron broad in front fifth, narrowing quite rapidly to middle, absent in apical half.

Ventral surface: Pronotal process arched in lateral view, highest point (viewed ventrally) between coxae, apical half parallel sided, tip weakly and bluntly pointed, narrowing between coxae, not reaching metathorax. Mesocoxae in contact in midline. Metathorax with a few small punctures; broadly triangular in midline in front; wings narrow; rounded behind in midline. Metacoxal plates sparsely punctate; metacoxal lines, relatively close, weakly diverging, reaching to about two thirds of way to mesosternum; adpressed to first abdominal ventrite. Metacoxal plates and first and second ventrites fused, other ventrites free, ventrites three and four with central group of setae, otherwise virtually without setae; virtually impunctate.

Legs: Protibia elongate about three times as broad at apex than at base; protarsi weakly expanded, second segment not much shorter than first, the fourth segment very small and hidden within deeply bilobed third segment, adhesive setae moderate; claws moderately strong. Mesotrochanter parallel sided, apex rounded with a few setae on inner edge; mesofemur with six strong setae on hind margin at base (Fig. 11); mesotarsi more elongate than protarsi. Metatrochanter large, inner edge curved, outer edge straight, rounded at tip, well separated from femur at apex (Fig. 12); metafemur narrow, anterior edge weakly sinuate, impunctate, without spines; metatibia strongly curved, thickening apically; metatarsal segments elongate, progressively shorter towards apical segment which is a little longer than penultimate, combined length of basal two segments approximately equal to other three; claws weak.

Male: Not known.

Etymology

The name pertains to Big Bell Mine which draws its water from the aquifer in which the species lives.

Remarks

At over three millimetres in length the largest *Nirridessus* so far known. It also is more rounded in outline and less flattened than most. The thin maxillary and labial palpi, narrow metafemur and strongly acute posterolateral angles of the pronotum also set it apart.

Additional Specimens

Taxon 1

One small (length 1.5 mm) female specimen was collected at Lake Violet. Although close to *N. hinkleri* it probably represents a distinct species. More specimens, including males are needed to confirm this.

'BES 7160, observation bore for Pump 5,

Wiluna Gold Lake Violet Borefield, 26°41'08"S, 120°13'05"E 8/5/99, coll. W. F. Humphreys & H. J. Hahn', slide mounted, WAM, registration number 26875.

Taxon 2

Eight partial specimens of a large species (approximately 4.0mm long.), together consisting of pronotum, abdomen, elytra and male genitalia, but lacking head and all appendages, were collected at Lake Way. These represent a distinctive species of uncertain generic placement.

'BES 7222, Sample 3 Site 289 Hinkler calcrete east, unequipped water bore, 26°51'36"S, 120°18'05"E, 22/5/99, coll. W. F. Humphreys & H. J. Hahn', 4 in spirit, WAM, registration numbers 26876, 26877, 26878, 26879. 4 slide mounted, SAMA.

Larvae

Larvae of two very different taxa were collected at Austin Downs (type 1) and Lake Violet (type 2). Although bidessine they differ considerably from the two larval taxa described in our earlier paper (Watts and Humphreys 1999). In comparison to epigean bidessine larvae we would consider the four larval taxa to be generically distinct. None appear to belong to the very small *Kintingka kurutjutu* Watts and Humphreys. This conclusion is in conflict with the adult taxonomy. Association of larvae and adults and more collecting will be needed to resolve this.

Type 1: 1, 'BES 7021, borefield monitoring bore PAT 2, Austin Downs Pastoral Station , 27°23'44"S, 117°42'25"E, 11/5/99', slide mounted, WAM, registration number 26880; 1, 'BES 7050, borefield monitoring bore PAT 7, Austin Downs Pastoral Station , 27°24'48"S, 117°2'40"E, 12/5/99', in spirit, SAMA; 1, 'BES 7055 borefield monitoring bore PAT 1, Austin Downs Pastoral Station , 27°23'19"S, 117°43'33"E, 12/5/99', slide mounted, SAMA.

Type 2: 10, 'BES 7148, observation bore for

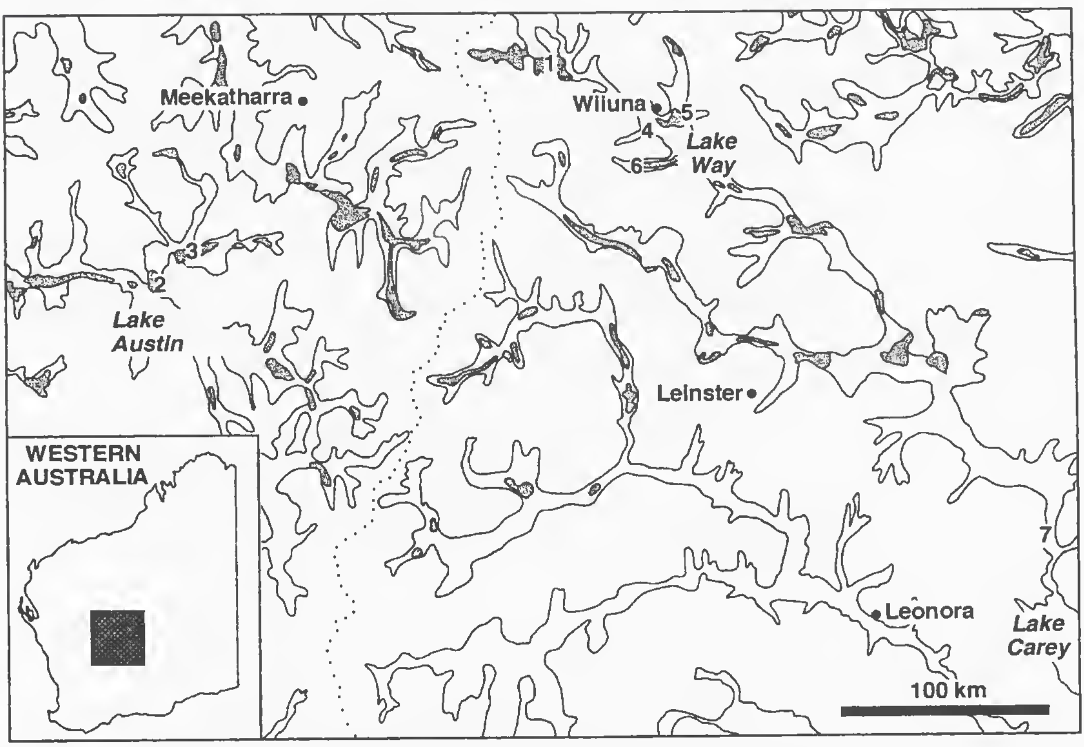


FIGURE 38. The distribution of stygal Dytiscidae in the Yilgarn Region. Groundwater calcrete deposits (shaded) are shown in the palaeodrainage channels (solid lines). The dotted line denotes the surface drainage divide (Beard 198); inland drainage to the east, Indian Ocean drainage to the west. The numerals denote discrete areas of calcrete (Table 1): 1, Paroo; 2, Austin Downs; 3, Cue; 4, Lake Violet; 5, North-east Lake Way; 6, Hinkler Well; 7, Mount Windarra.

TABLE 1. The distribution of stygal species of dytiscids amongst discrete calcrete bodies in the Yilgarn district of Western Australia.

Genus Calcrete body	*Tjirtudessus* W & H	*Nirridessus* W & H	*Kintingka* W & H
Western drainage			
Austin Downs	–	*bigbellensis* sp. nov.	–
Cue	[4]*magnificus* sp. nov.	[4]*cueensis* sp. nov.	–
Eastern drainage			
Paroo	[2]*eberhardi* W & H[1]	[2]*pulpa* W & H	[2]*kurutjutu* W & H
Lake Violet	–	undescribed sp.	–
NE Lake Way	*hahni* sp. nov.	*morgani* sp. nov.	–
Hinkler Well	–	*hinkleri* sp. nov.	–
Mount Windarra	[3]*lapostaae* W & H	[3]*windarraensis* W & H	–

[1] W & H = Watts & Humphreys 1999; [2] sympatric; [3] sympatric; [4]sympatric.

Pump 1, Wiluna Gold Lake Violet Borefield , 26°40'30"S, 120°13'55"E, 18/5/99'. 4 WAM, registration numbers 26881, 26882, 16883, 16884, 6 SAMA, slide mounted and in spirit; 1, same data but 'BES 7231, WAM, registration number 26885; 1, same data but 'BES 7242', WAM, registration number 26886. All collected by W. F. Humphreys and H. J. Hahn.

Discussion

Distribution

Dytiscid specimens were collected from six separate calcrete deposits: 1, Austin Downs (borefield for Big Bell Gold Mine); 2, Cue (former borefield for the town of Cue); 3, Paroo (pastoral station, detailed in Watts and Humphreys 1999); 4, Lake Violet at the northern end of Lake Way contains the borefield for Wiluna Gold Mine; 5, the Hinkler Well calcrete, the hydrogeochemistry of which is detailed in Mann and Deutscher (1978); and 6, the northeastern side of Lake Way adjacent to the Lakeway Uranium prospect (DCE 1981) (Fig. 38). Sites 1 and 2 drain towards the Indian Ocean whilst the remainder are to the east of the drainage divide in the Carey palaeodrainage system (sensu Morgan 1993) which drains to the interior of the continent. The distribution of the taxa by calcrete body is shown in Table 1.

No dytiscids or other large stygofauna were taken from open, hand dug, pastoral wells even if they were adjacent to narrow bores containing stygal dytiscids and other stygofauna. Despite sampling widely in non-calcrete aquifers no dytiscids were collected in other than calcrete aquifers, which confirms the conclusion of our earlier, much more restricted sampling, that the beetle and other larger stygofauna is restricted to aquifers in areas of calcrete (W. F. Humphreys unpublished; Watts and Humphreys 1999). In addition, this study extends the range of waters inhabited by stygal dytiscids, and other stygofauna, to saline water with a salinity of at least 20 g l^{-1}.

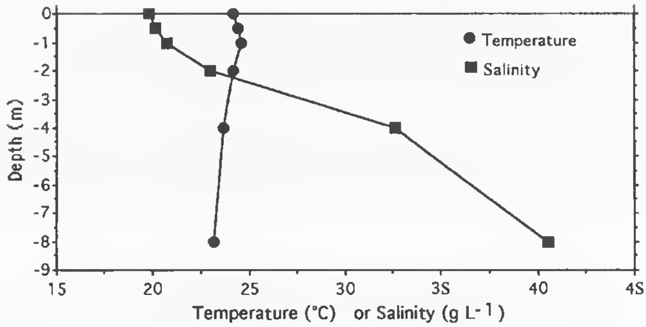
These discoveries significantly extend the known range of both *Tjirtudessus* and *Nirridessus* from the inland draining Lake Way/Lake Carey palaeodrainage channel to the seemingly never-connected Murchison palaeodrainage system that drains westward to the Indian Ocean. No Dytiscidae were discovered in stygofauna-rich calcrete aquifers in the Pilbara region. Since only about 9% of the major calcrete deposits in the palaeodrainage channels of Western Australia alone (Humphreys 1999) have been sampled for stygofauna it is likely that additional subterranean Dytiscidae remain to be discovered in Australia.

Associated fauna

The dytiscids were collected amongst a diverse stygofauna comprising mainly phreodrillid Oligochaeta, bathynellids (Syncarida), Ostracoda, cyclopoid and harpacticoid Copepoda, crangonyctoid and ceinid Amphipoda and *Haloniscus* (Oniscoidea: Isopoda).

Water quality

Fresh to saline groundwaters occur widely in calcretes and may be reached as close as two metres from the surface to more than 100 m below the surface. The calcrete aquifer itself may vary up to 30 m in thickness (Barnett and Commander



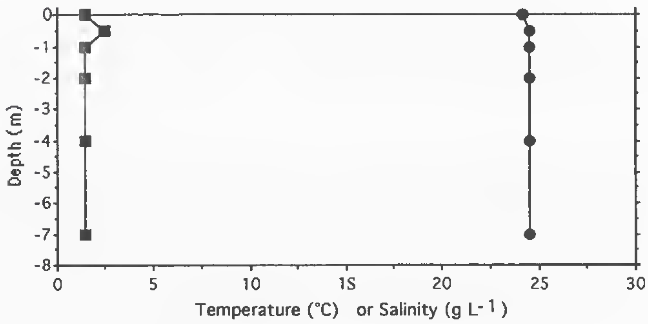


FIGURE 39. Physiochemical profiles in some aquifers from which dytiscid beetles were collected. Upper, site 286 NE Lake Way; lower, site 289 Hinkler East.

1985), but those sampled in the Yilgarn are typically thin and the groundwater is close to the surface (Table 2). The area is arid and rainfall (c. 200 mm per year) is irregular predominately as episodic heavy falls (Sanders 1973) which recharge the calcrete aquifers through the porous, often karstic (Barnett and Commander 1985), surfaces. Indeed, groundwater calcretes are carbonate deposits forming near the water table in arid lands as a result of concentration processes by near-surface evaporation and they are associated with slow moving groundwater that fluctuates widely in depth (Jacobson and Arakel 1986; Morgan 1993). In consequence the groundwater table varies quite widely between storm events and markedly in salinity. The dytiscids were collected from water of variable quality (Table 2) with samples collected from fresh water (salinity < 1000 mg l^{-1}) as well as saline conditions (salinity > 20 000 mg l^{-1}). At some locations the water was well stratified with marked changes in the physico-chemical conditions with depth, while at others the vertical profile was less marked (Fig. 39; Table 2).

Considerable seasonal variation occurs in the salinity of at least some of the habitats (foot note to table 2) but the effect of this on the distribution of the stygofauna is unknown. Marked seasonal changes in numbers have been reported for stygal dytiscids inhabiting alluvial aquifers near rivers (Ordish 1976), and it is known that changes to the water table and the direction of groundwater flow have profound effects on the location of such populations (Richoux and Reygrobellet 1986).

Palaeogeography and hydrology

While much is still to be learnt of these stygal dytiscids, it is worthwhile at this stage to consider the palaeogeographic and hydrological setting in which this fauna, and that reported by Watts and Humphreys (1999), occurs.

The Western Shield of Western Australia is divided from north to south by a drainage divide that separates the rivers, some still active, draining to the Indian Ocean, from those draining to the east and which are now largely inactive and disorganised (Beard 1998). The present drainage, now mostly a palaeodrainage system, formed during the Mesozoic when the Western Shield was attached to Antarctica (Beard 1998; van de Graaf *et al.* 1977; Morgan 1993). The sediments infilling the palaeochannels are mostly Eocene or later but the age of the calcretes is unknown. Morgan

TABLE 2. Physico-chemical characteristics of sites from which stygal dytiscids were recorded.

Site	Sample depth (m)	Salinity g L	Temperature °C	Dissolved O_2 % sat	mg L^{-1}	pH	[2]Depth to water (m)	[2]Depth of water(m)
PAT2 – Austin Downs	–	5[1]	–	–	–	–	4.8	6
PAT1 – Austin Downs	–	8[1]	–	–	–	–	8	4.8
Old Cue town bore	–	5	25	50.5	3.9	–	4	0.5
GSWA5 surface- Paroo	–	1.38	26.7	59.7	4.5	7.7	3.6	[3]4
GSWA5 deep- Paroo	–	–	–	49	3.7	–	–	–
GSWA6 surface- Paroo	–	0.77	24.8	59.7	4.6	7.5	5	[3]6.6
GSWA6 deep- Paroo	–	0.79	24.7	43.5	3.4	7.5	–	–
GSWA15 small- Paroo	–	0.53	26	59.2	4.5	8.4	3	[3]8
GSWA15 small- Paroo	–	0.6	25.3	38.6	3	7.9	–	–
SB 32/1 – Hinkler west	–	1.66	26.9	79.2	6	7.7	4.8	2
TPB 25/4 – Hinkler west	–	2	–	–	–	–	4.8	34
OB Pump 1 – Lake Violet	–	2.36	24.6	88.7	7	8.2	4.8	5.6
262 – NE Lake Way	–	4.46	25.7	86.1	6.6	7.6	4	1.6
286 – NE Lake Way	0	19.8	24.2	23	1.8	–	2	20
286	0.5	20.1	24.4	–	–	–	–	–
286	1	20.7	24.6	–	–	–	–	–
286	2	23	24.2	–	–	–	–	–
286	4	32.6	23.7	–	–	–	–	–
286	8	40.5	23.2	–	–	–	–	–
288 – Hinkler east	0	1.46	24.2	68.6	5.4	8.3	2.4	19
288	0.5	2.43	24.5	–	–	–	–	–
288	1	1.43	24.5	–	–	–	–	–
288	2	1.42	24.5	–	–	–	–	–
288	4	1.42	24.5	–	–	–	–	–
288	7	1.42	24.5	–	–	–	–	–
289 – Hinkler east	0	1.56	24.4	74.4	5.9	8	2.4	19
289	0.5	1.7	24.6	–	–	–	–	–
289	1	2.04	24.5	–	–	–	–	–
289	2	2.1	24.5	–	–	–	–	–
289	4	2.12	24.5	–	–	–	–	–
289	8	2.15	24.5	–	–	–	–	–

[1] PAT1 and PAT2 have annual salinity variation between 5–9 g l^{-1} and 5–22 g l^{-1} respectively as determined from borefield monitoring by Big Bell Mine. [2] Depth approximate. [3]To base of calcrete (Sanders 1972).

(1993) considered it likely that they formed from the start of the Oligocene following the onset of the continental aridity but they have probably been remobilized and redeposited. As this process is continuing it is not possible to date the calcretes using standard radiometric methods.

The Yilgarn Craton covers 750,000 km^2 of southwestern Australia between latitudes 34° and 25° S and has mostly not been submerged by the sea since the beginning of the Mesozoic. The northeastern half is semi-arid with unreliable rainfall that may fall throughout the year.

The central watershed traverses a palaeosurface barely modified since the Cretaceous (Beard 1998). This central watershed is of fairly uniform elevation traversed only by a few minor gaps or low points that may be indicative of a change to the drainage patterns in the distant past. One of these is on Killara Station where a col, 50–100 m below the level of the adjacent watershed, separates the Murchison and the Carey (Lake Way-Lake Carey in Watts and Humphreys 1999) palaeodrainage systems (Beard 1998) which together encompass the entire distribution of the Australian stygal dytiscids known to this time. While it is tempting to invoke some significance of this gap to the biogeography of the stygofauna, this minor gap may merely reflect the trend of less resistant Proterozoic rocks (Beard 1998).

The collection sites at Cue and Lake Austin

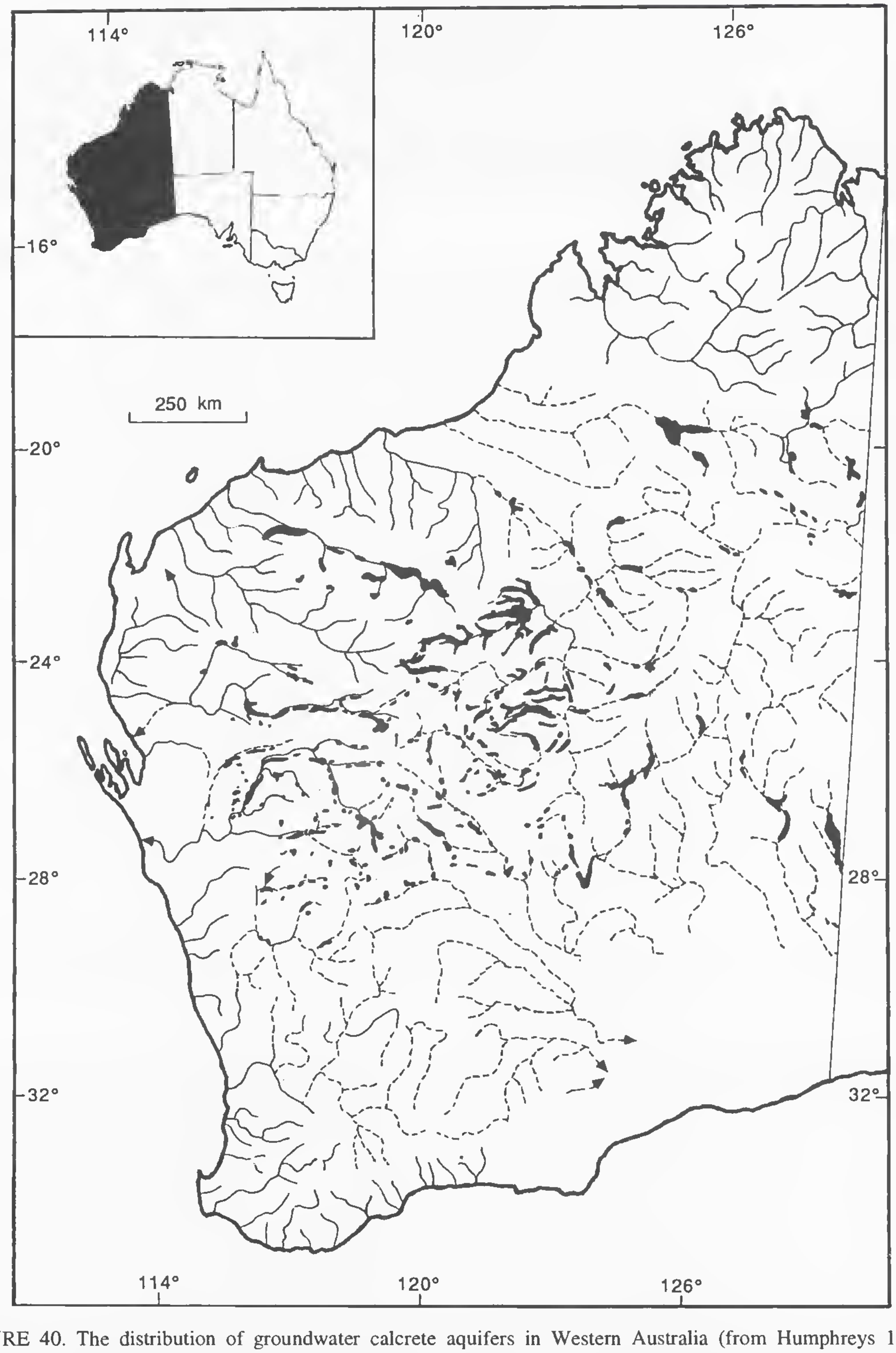


FIGURE 40. The distribution of groundwater calcrete aquifers in Western Australia (from Humphreys 1999). Modern and palaeo-drainage (respectively, continuous and dashed lines) and calcrete areas (black) are shown. Derived from data in Geological Survey (1989), drawn by Julianne Waldock on a base map provided by Philip Commander (further details in Humphreys 1999).

(containing *Tjirtudessus magnificus*, *Nirridessus cueensis* and *Nirridessus bigbellensis*) are separated from those to the east (containing *Tjirtudessus hahni*, *Nirridessus hinkleri* and *Nirridessus morgani* plus the five species in Watts and Humphreys 1999) by the continental water divide (Beard 1998) between the inland drainage and that draining to the Indian Ocean. As the water divide is also the approximate water divide for the palaeodrainage systems that date from at least the Cretaceous no subterranean hydrological connection is likely to have occurred. The presence of congeneric stygal species on either side of this water divide suggests that the fauna colonised groundwater from a widespread epigean ancestor, possibly driven by the increasing aridity of central Australia since the Eocene.

Groundwater calcretes stretch through arid central Australia as far as the border of the Northern Territory and Queensland (Fig. 40; Humphreys 1999). Similar calcretes occur on the Pilbara Craton which comprises much of the rest of the Western Shield of Australia, and there also, each discrete calcrete area sampled so far contains a distinct stygofauna (Poore and Humphreys; W. F. Humphreys and S. M. Eberhard, unpublished; S. M. Eberhard, unpublished; S. M. Eberhard and W. F. Humphreys unpublished). However, no dytiscids have been taken from the Pilbara Craton.

Each of the seven discrete, but sometimes adjacent, calcrete areas sampled from the palaeodrainage lines on the Yilgarn Craton (herein and Watts and Humphreys 1999) contains a distinct assemblage of dytiscids (and probably other stygofauna). The data represented here contains samples from only two of 42 major calcretes areas in the upper Murchison catchment, and five out of 18 major calcrete areas in the Carey palaeodrainage system. In Western Australia alone there are about 210 major calcrete areas divided amongst about five major drainage systems (Fig. 40)

Each calcrete sampled in the Yilgarn (and Pilbara) containing stygofauna has a unique stygofaunal community and as only a small proportion of the available calcrete areas have been sampled, this suggests that there is considerable biodiversity to be unearthed amongst the dytiscids and in the arid zone stygofauna generally.

Changes to the water table and the direction of groundwater flow may have profound effects on the location of populations of stygal dytiscids (Richoux and Reygrobellet 1986) and unique stygal assemblages, including Dytiscidae, may be lost if groundwater pollution occurs (Uéno 1996). As the stygofaunas are unique with circumscribed distributions and they occur in systems of potential or actual resource developments, they present a real challenge for innovative environmental management. Furthermore, these calcrete aquifers are sufficiently replicated and contain a diversity of fauna sufficient to test independently theories and processes that gave rise to the vicariance within these systems.

While much work is needed to start to understand distribution patterns, the faunistic distinctiveness of the groundwater calcrete aquifers is consistent with the evolution of the hydrogeological system in the palaeodrainage channels as interpreted by Morgan (1993). In essence, Morgan argues that in the palaeorivers north of latitude 30°S separate geochemical systems develop associated with the formation of each salt lake (playa) along a palaeodrainage system. In the groundwater there is a well defined change in common ion ratios developed with increasing salinity marked especially by a relative increase in chloride and sulphate with respect to other ions—this may contribute to the heterogeneity in stygofauna distribution within a given calcrete area reported by Poore and Humphreys (1998). As it is related to the rate of movement of the groundwater, this increase in salinity and relative chloride/sulphate content is both spatial and temporal because the change takes place between widely separate intake and outflow locations. This hydrochemical trend commences at the headwaters of each recharge system, such as a large alluvial fan, and completes its cycle at the evaporation outlet marked by the lower boundary of the calcrete with a salt lake. The main channel calcretes are formed at the downstream end of an individual hydrochemical system and immediately upstream of an evaporation outflow area forming a salt lake (Morgan 1993). Several similar hydrochemical cycles may occur along a single palaeodrainage system.

The marked age and stability of the palaeodrainage systems themselves, coupled with the repeated cycles of fresh to hypersaline (>200 g l^{-1}) groundwaters along the length of each palaeodrainage system would effectively isolate each stygal assemblage within the region where groundwater characteristics are suitable for their development.

Acknowledgments

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